Estimation of Variance Components for Nordic Red Cattle Test-Day Model: Bayesian Gibbs Sampler vs. Monte Carlo EM REML

M.H. Lidauer¹, P. Madsen², K. Matilainen¹, E.A. Mäntysaari¹, I. Strandén¹, R. Thompson³,

J. Pösö⁴, J. Pedersen⁵, U.S. Nielsen⁵, J.-Å. Eriksson⁶, K. Johansson⁶, G.P. Aamand⁷

¹MTT Agrifood Research Finland, Biotechnology and Food Research, Biometrical Genetics, Jokioinen, Finland; ²Danish Institute of Agricultural Sciences, Genetics and Biotechnology, Foulum, Denmark; ³Rothamsted

Research, Biomathematics and Bioinformatics, Harpenden, United Kingdom; ⁴Faba Breeding, Vantaa, Finland;

⁵The Danish Agricultural Advisory, Aarhus, Denmark; ⁶Swedish Dairy Association, Stockholm, Sweden; ⁷NAV Nordic Cattle Genetic Evaluation, Aarhus, Denmark

1. Introduction

Genetic evaluation of yield traits for the dairy breeds in Denmark, Finland and Sweden is based on a multi-breed multi-lactation random regression (RR) test-day (TD) model, which allows different heritabilities for each breed. Currently used variance components (VC) were estimated in 1998 and 2001 and therefore a re-estimation of the VC was desirable. The VC analyses were conducted by Bayesian methods (Madsen *et al.*, 2008). Post Gibbs analyses showed poor mixing properties for several VC, which left us uncertain about the quality of the parameters estimated.

Bayesian analysis is favoured in many RR VC studies (Jamrozik et al., 2001) as it allows a simultaneous estimation of all parameters. For RR models, benefits of exact REML methods are stalled by the need of the inverse of a large coefficient matrix. Consequently, VC for large RR models are acquired by summing estimates from analyses of many subsets (Thompson et al., 2005). García-Cortés et al. (1992) showed that inversion of the coefficient matrix can be circumvented by Monte Carlo (MC) re-sampling for prediction error variances. In an ongoing Ph.D. study, ideas of García-Cortés et al. (1992) are developed for a multivariate EM REML implementation (Matilainen et al., 2009).

Aim of this study was to compare Bayesian RR VC estimates for Finnish Ayrshire (FAY), Swedish Red Breed (SRB) and Danish Red Cattle (RDM), with estimates obtained by the multivariate EM REML algorithm.

2. Estimation of parameters

2.1 Data and model

TD observations on milk, protein and fat yield from the first three lactations were selected from 19709, 19928 and 19857 cows of the three main breeds FAY, SRB and RDM, respectively, calving from 1995 to 2006. The three data samples comprised of 374009, 353340 and 320881 TD records. For FAY, protein and fat were only available on every second TD. The amounts of data were found large enough to infer about differences in heritabilities across breeds (Madsen *et al.*, 2008). The chosen multiple-trait RR animal model was:

$$y_{ijkmnoqrt} = H_{ijt} + A_{kt} + D_{mt} + \sum_{r=0}^{4} M_{jrt} \varphi_r(d) + h_{int} + \sum_{r=1}^{3} c_{ijtr} \lambda_r(d) + \sum_{r=0}^{3} a_{otr} \lambda_r(d) + \sum_{r=0}^{3} p_{otr} \lambda_r(d) + e(s)_{ijkmnoqt}.$$

Fixed effects were herd×2-years-calvingperiod (H), calving age (A), days carried calf (D) and regressions on days in milk (DIM) (d) within 2-years calving period (M). Random effects were herd test-day (h), RR for herd \times 2years calving period (c), additive genetic (a), and non-genetic (*p*) effects. The random error block diagonal, *(e)* was with blocks corresponding to lactation, and nested within 12 DIM classes (s), from d=8 to d=365 with different intervals: 3×2 weeks, 3×3 weeks, $3 \times$ 7 weeks, and 3×5 weeks. Lactation curves were fitted by Legendre polynomials of d plus a Wilmink term W=exp(-0.04d) giving L_0, L_1 ,

 L_2 , L_3 and W nested within M; L_1 , L_2 , and W nested within c; L_0 , L_1 , L_2 , and W nested within a and p. Size of (co)variance matrix was 9×9, 27×27, 36×36 and 36×36 for h, c, a, and p, respectively. In total, 1971 VC parameters were estimated for each breed.

2.2 Bayesian analysis via Gibbs sampler

Bayesian analysis was conducted by a Gibbs sampler implemented in the DMU-package (Madsen & Jensen, 2008). Flat priors were assumed for fixed effects and Wishart distributions for all random effects. Prior values for VC were obtained from analysis of samples of TD records from ~1000 cows. The degree of belief was set to dimension of the covariance matrix + 2 to make priors proper. A post Gibbs analysis was conducted to determine burn-in period and calculate for each parameter the effective sample size (ESS). Initial sequence estimators for ESS were calculated as given by Geyer (1992).

2.3. Monte Carlo EM REML analysis

The Monte Carlo expectation maximisation (MC-EM) REML algorithm, presented by (García-Cortés et al., 1992), was developed further. The implementation allows multivariate analysis with missing observations. Solving the random effects was based on the MiX99 package (Vuori et al., 2006). In each REML round, the algorithm requires calculation of sums of squares from BLUP solutions of the real data and of sampled data. Two sampled data sets in each REML round were found sufficient for these analyses. The convergence was examined using the relative change in round to round linear regression predictors of the VC estimates. A detailed description of the MC-EM REML implementation will be given by Matilainen et al. (2009) at the forthcoming EAAP meeting in Barcelona.

3. Results

Available chains from the Bayesian analyses were of length 269720, 246840 and 189800 for FAY, SRB and RDM, respectively. First 70000 samples were discarded as burn-in and every 20th sample from the remaining chain was used. This yielded 9984, 8840 and 5990 samples, respectively, which were used for the calculation of ESS and posterior means. ESS were high for herd test-day, herd-curve and residual effect VC, sufficiently high for nongenetic animal effect VC, but low for the additive genetic animal effect VC (Table 1).

Table 1. Averag	ge effective	sample	size for	the
estimated VC by	random ef	fect and	breed.	

••••••••••	runuom er		
(Co)Variances		Swedish	Red
Estimates for	Finnish	Red	Danish
Random Effect	Ayrshire	Breed	Cattle
Herd test-day	6855.8	6460.7	3164.6
Herd curve	2659.5	2942.8	2345.6
Non-genetic	290.3	164.9	225.7
animal			
Additive	57.2	42.8	42.6
genetic			
Residual	7231.5	7117.5	4752.7

For each of the MC-EM REML analyses 3000 REML rounds were performed. Study of convergence suggested a value $\leq 1.0 \times 10^{-8}$ for the applied criteria to ensure sufficient convergence. This value was reached fastest by the herd test-day VC estimates and slowest by the non-genetic and additive genetic animal VC estimates (Table 2).

Table 2. Number of REML rounds to reach convergence given by random effect and breed.

(Co)Variances		Swedish	Red
Estimates for	Finnish	Red	Danish
Random Effect	Ayrshire	Breed	Cattle
Herd test-day	164	131	159
Herd curve	466	566	451
Non-genetic	2075	2535	>3000*
animal			
Additive	1576	1954	2397
genetic			
Residual	1652	609	462

converged to 1.7×10^{-8}

3.1 Differences in VC estimates

Overall, estimated VC from the both methods were in good agreement when estimates had high ESS in the Bayesian analysis. Significant differences were found for genetic animal effect covariances, which included a Wilmink term (Figure 1, Table 3). For FAY milk yield, some estimates for non-genetic animal and additive genetic animal effects were different between the both methods although the ESS was high. The variance estimate for L_0 of 1st

lactation milk yield was 1.887 and 1.990 from Bayesian and the MC-EM REML analysis, respectively. The difference was not explained by differences in mean and mode of the posterior distribution (posterior mode was 1.902).



Figure 1. Plot of samples (Bayesian analysis) and convergence (MC-EM REML analysis) for three genetic covariance parameter estimates for Swedish Red Breed.

biecu.										
	Finnish Ayrshire			Sw	Swedish Red Breed			Danish Red Cattle		
		Milk 1, L_0			Milk 1, L_0			Milk 1, L_0		
	ESS	GS	REML	ESS	GS	REML	ESS	GS	REML	
Milk 2 L_0	124.5	1.799	1.758	200.0	2.119	2.016	22.4	1.810	1.765	
L_{I}	162.9	0.067	0.027	154.4	0.318	0.233	45.0	0.186	0.145	
L_2	54.1	-0.204	-0.232	93.5	-0.271	-0.243	20.2	-0.146	-0.010	
W	22.7	-0.562	-0.574	24.1	-0.478	-0.684	20.4	-0.519	-1.302	
Protein 2 L_0	125.9	1.000	0.955	198.5	1.289	1.240	21.9	1.104	1.080	
L_{I}	179.6	0.267	0.235	144.9	0.457	0.376	63.7	0.351	0.308	
L_2	63.6	-0.138	-0.129	96.4	-0.155	-0.147	19.5	-0.075	0.029	
W	21.7	0.457	0.355	26.8	0.461	0.248	20.4	0.332	-0.307	
Fat 2 L_0	142.8	0.669	0.638	163.6	0.913	0.871	36.5	0.682	0.682	
L_{I}	139.3	0.179	0.186	123.9	0.322	0.282	54.2	0.261	0.213	
L_2	78.6	-0.069	-0.061	61.3	-0.079	-0.088	39.0	-0.030	0.057	
W	23.1	0.171	0.175	16.4	0.024	0.013	53.3	0.028	-0.553	

Table 3. Effective sample size (ESS), posterior mean from Gibbs sampler (GS) and REML estimate for genetic covariances between intercept of first lactation milk and second lactation parameters by breed.

3.2 Correlations

Genetic correlations between different DIM within and across traits were the same or somewhat lower when VC were estimated with MC-EM REML (Figure 2). However, derived 305d genetic correlations between traits differed not more than ± 1 percent point between the estimation methods. Phenotypic correlations between different DIM within and across traits were practically the same from both VC estimation methods and all breeds.

3.3 Heritabilities

Daily heritabilities obtained from the both methods were in good agreement for RDM and SRB (Figure 3). For FAY, heritabilities were in good agreement for protein and fat yield traits, but showed some differences for milk yield traits. Daily heritabilities for these traits were on average 10% lower when VC were estimated by the Gibbs sampler. These differences are also seen in heritabilities given on a 305-d base (Table 3).



Figure 2. Genetic (above) and phenotypic (below) correlations between DIM 60 of 1st lactation protein yield and all other DIMs and traits given for Swedish Red Breed by VC estimation method.



Figure 3. Daily heritabilities for Swedish Red Breed by VC estimation method.

Table 3. Heritabilities given on 305-d base, derived from VC estimated by Gibbs sampling (GS) or MC-EM REML (REML) for milk (M), protein (P), and fat yield (F) of 1^{st} (1), 2^{nd} (2), and 3^{rd} (3) lactation by breed; Finnish Ayrshire (FAY), Swedish Red Breed (SRB), and Danish Red Cattle (RDM).

	FAY		SRB		RDM	
	GS	REML	GS	REML	GS	REML
M1	0.35	0.38	0.44	0.44	0.42	0.42
P1	0.32	0.33	0.43	0.43	0.39	0.38
F1	0.34	0.35	0.43	0.43	0.40	0.39
M2	0.31	0.33	0.33	0.33	0.36	0.35
P2	0.32	0.32	0.36	0.34	0.36	0.35
F2	0.33	0.34	0.36	0.34	0.35	0.35
M3	0.29	0.31	0.32	0.34	0.36	0.34
P3	0.29	0.31	0.35	0.35	0.37	0.35
F3	0.33	0.33	0.36	0.36	0.37	0.35

4. Discussion

Madsen et al. (2008) observed poor mixing in daily heritability estimates in a post Gibbs analysis of first 100000 samples from a similar RR VC analysis for Holstein. The problems were compensated by a longer burn-in period. In this study, Gibbs sampler chains were considerably longer, which allowed to discard first 70 000 samples. Estimated daily heritabilities were in good agreement with those obtained from the MC-EM REML analyses. Whether lower heritability estimates for FAY milk yield were due to the data structure, with protein and fat recording at every second TD only, has to be investigated closer. Differences in parameter estimates

between the both VC estimation methods were mainly found for genetic parameters for which ESS were low in the Bayesian analysis. These parameters converged slowly in the MC-EM REML analyses as well. MC-EM REML showed robust convergence behaviour but required between 2000 to 3000 rounds to ensure for all parameters convergence. Nevertheless, MC-EM REML was superior in computing time. Analysis of FAY required for one EM round 17.1 min, which was equal to computing time need for eleven Gibbs sampler rounds. Total computing times for FAY analyses were 35 days by the MC-EM REML and 282 days by the Gibbs sampler. An advantage of Gibbs sampling is that posterior standard derivations for VC and functions of VC can be obtained.

5. Conclusions

Variance component estimates for large RR TD models were in good agreement between the two applied VC estimation methods; Bayesian analysis *via* Gibbs sampler, and MC-EM REML. The implemented MC-EM REML algorithm was superior in computing time to the Gibbs sampler and has shown its potential to become the method of choice in future VC analysis of complex models.

6. Acknowledgement

Further development and implementation of the Monte Carlo EM REML algorithm is part of an ongoing Ph.D. study financed by Rothamsted Research and MTT.

References

- García-Cortés, L.A., Moreno, C., Varona, L. & Altarriba, J. 1992. Variance component estimation by resampling. *J. Anim. Breed. Genet. 109*, 358-363.
- Geyer, C.J. 1992. Practical Markov chain Monte Carlo. *Stat. Sci.* 7, 473-511.
- Jamrozik, J., Gianola, D. & Schaeffer, L.R. 2001. Bayesian estimation of genetic parameters for test day records in dairy cattle using linear hierarchical models. *Livest. Prod. Sci. 71*, 223-240.
- Madsen, P. & Jensen, J. 2008. A Users's Guide to DMU. A package for analysing multivariate mixed models. Version 6,release 4.7. Faculty of Agricultural Sciences, University of Aarhus. Denmark. 33 pp.
- Madsen, P., Lidauer, M.H. & Mäntysaari, E.A. 2008. Strategy for estimation of variance components for the joint Nordic yield evaluation. *Interbull Bulletin 38*, 36-39.
- Matilainen, K., Lidauer, M., Strandén, I., Thompson, R. & Mäntysaari, E.A. 2009. Comparison of Monte Carlo EM REML and Bayesian estimation by Gibbs sampling in estimation of genetic parameters for a test day model. In *Proceedings of the* 60th *Annual Meeting EAAP, Barcelona, Spain, August 24-27 2009.*
- Thompson, R., Brotherstone, S. & White, I.M.S. 2005. Estimation of quantitative genetic parameters. *Phil. Trans. R. Soc. B* (2005), 360, 1469-1477.
- Vuori, K., Strandén, I., Lidauer, M. & Mäntysaari, E. A. 2006. MiX99 – Effective solver for large and complex mixed models. *Proc. 8th World Congr. Genet. Appl. Livest. Prod.*, August 13-18, 2006, Belo Horizonte, MG, Brazil. Proceedings CD.